CIRCUM-ANTARCTIC DISTRIBUTION PATTERNS AND CONTINENTAL DRIFT

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CONTENTS

1. — INTRODUCTION

The present symposium is devoted to the problem if there are causal connections between recent intercontinental distribution patterns and Mesozoic geography. The problem is far from new but of high actuality today, when the theory of continental drift is getting generally accepted by geologists and geophysists. However, we are dealing here with nothing more than a theory, even though it seems very well founded and has given rise, during the past five years, to the new theory of plate tectonics. Here the historical biogeographer cannot simply accept or dismiss. As a paleogeographer he remains an outsider. It is his duty to approach the matter as an evolutionist, without prejudice; and he must be fully aware that the weight of his biological contribution is proportionate to the consistency of his application of the principles of phylogenetic biogeography.

2. — PRINCIPLES OF PHYLOGENETIC BIOGEOGRAPHY

The primary reason for the still remaining uncertainty as to the meaning of many intercontinental distribution patterns is insufficient knowledge of the structure of the phylogenetic relationships existing between the disjunct or more or less overlapping subgroups of an actual group. Moreover, it seems still not to be generally perceived that a further demand for a realistic discussion of the history in time and space of a group is knowledge of the sister group.

Phylogenetic biogeography is the study of the history in time and space of the supraspecific evolutionary units, i.e., the monophyletic species groups.

This definition is a consequence of our insight that nature has created a system of its own that is in principle hierarchic. The units of this truly phylogenetic system are the biological species and

the strictly monophyletic species groups all of which have individuality and reality. Hence it is clear that dispersal and evolutionary change have been realized in time and space within orderly hierarchical sequences of successively subordinate monophyletic groups. Without proper reconstruction of the latter, we cannot make a realistic reconstruction of the history of life in time and space.

For the reconstruction we have to resort to a three-step procedure comprising (1) a broad comparative study of the character patterns of the world fauna of a group, (2) investigation of the position of homologous characters in transformation series (the anagenetic analysis), and (3) the phylogenetic-biogeographical synthesis. The latter includes establishment of strict monophyly by exclusive use of synapomorphy, i.e., joint possession of unique specializations, and search for sister groups by additional use of the geographical distribution of the actual species. It is the correlated pattern of *geographical replacement* displayed by the reconstructed sister-group system that elucidates the history in time and space of a group.

However, proper conclusions as to areas of origin and directions of dispersal cannot be performed without additional application of the principle that *dispersal*, seen in the time perspective, is a multiple process including progression in space, evolutionary change (i.e., development of comparative derivativeness), and speciation by cleavage of an ancestral gene pool. It is because of this insight that we are able to establish the fundamental biogeographical principle that a primitive group at least primarily is closer to the area once occupied by the ancestral species than is the comparatively derivative sister group.

Misinterpretations of the causal connections involved here are the reason for the old and widespread conception (still maintained by Darlington, 1965) that the southern continents have functioned as receivers and preservers of old, primitive groups driven southwards from a northern continental block that has functioned as a constant cradle for new, progressive groups. This line of thought means a violation of the principles of dispersal and speciation. Indeed, phylogenetic evolution in time and space cannot be compared with the wave pattern that is formed when a stone is thrown into the water and where the first-born waves are peripheral. Multiplication of species is normally the result of unequal cleavage of the gene pool of a stem species (cf. Brundin, 1972 *b*), and a comparatively derivative species (species group) is just as old as its primitive sister species (group).

Widespread is also the view that the history of a group cannot be reconstructed without support of a comprehensive fossil record. This is only partly true and valid foremost for old relict groups poor in species, for example, Monotremata, *Sphenodon*, *Leiopelma*, where informative patterns of geographical replacement are not available (Brundin, 1972 *a*). When asking for fossils the biologist often seems to forget that adequate use of a fossil requires *previous reconstruction* of the hierarchy formed by the recent species of the actual group. On the other hand, even if that requirement would be fulfilled, a fossil very rarely is so well preserved that its position in the phylogenetic hierarchy can be exactly established (cf. Hennig, 1969). As a matter of fact, the accessibility of a group to phylogenetic-biogeographical synthesis is different for different reasons, and a good fossil record is not necessarily more important than several other prerequisites (cf. Brundin, 1966 : 438-439 ; 1967 ; 1972 *a*).

Finally, another general consideration. The biota of the different continents consist of elements of different age and with a different history ; but practically every element is composed of faunal and floral components with a common history in time and space. Hence it can be anticipated that a reconstruction of the history of a few components will mirror some of the main trends in the history of a whole biogeographical element, no matter whether the objects selected are plants or animals, insects or birds. Facing the immense time perspective involved in the history of groups of Mesozoic age, it would evidently be delusive to suppose that different means of dispersal have played an appreciable role for the development of the great intercontinental distribution patterns. Continental faunas and floras seem to move together, step by step. Successful long-distance dispersal by one or a few individuals is a marginal phenomenon that cannot influence the main patterns. As to these matters, I wish to refer especially to the comprehensive and eloquent works of Croizat (1958, 1960, 1962, 1968).

3. — MAIN PATTERNS OF TRANSANTARCTIC RELATIONSHIPS

Since the time of Darwin, Hooker and Wallace, the history behind the circum-Antarctic distribution patterns has been one of the great problems of historical biogeography. How can it be that so many southern plant and animal groups are represented by subordinate groups in southern South America, Australia, New Zealand, and, sometimes, also southern Africa, areas that are now separated by vast expanses of sea and a great ice-covered continent ?

The botanist Joseph Hooker, who had a more intimate survey of the matter, based on personal field work, than any of his contemporaries, arrived at the view (in 1853) that there has been an important centre of evolution in the south, and that the present disjunct groups all are members of a once more extensive southern flora, which has been broken up by geological and climatic causes. Hooker's view has been contended by many later biogeographers, independently of their attitude to the theory of Wegener. However, most biogeographers seem to have been firm believers in the permanency of the geographical main features. According to them the circum-Antarctic distribution patterns are the result either of accidental long-distance dispersal in the south, partly via subantarctic islands and an ice-free Antarctic continent, or of independent dispersal from the north.

The faithful adherence to incompatible explanations by different camps alluded to above, which has been one of the main characteristics of traditional biogeography, is closely connected with the general use of inconclusive arguments. The acceptance of the principles of phylogenetic systematics introduced by Hennig (1950, 1953, 1957, 1966 *a*) is still in its infancy. It is a remarkable fact, however, that all biogeographical applications on a major scale of those principles that have been made as yet, refer to limnic arthropods and have been devoted more or less directly to the problem of transantarctic relationships. There are significant reasons (Brundin, in press) for the accordant concentration of these recent biogeographical efforts, which refer to the following works : Best, 1964 (Hydrachnellae) ; Brundin, 1963, 1965, 1966, 1967, 1970, 1972 *a*, (Diptera, Chironomidae) ; Illies, 1960, 1961, 1963, 1965 *a*, *b*, *c*, (Plecoptera) ; Schminke, 1973 *a b* (Syncarida, Bathynellacea). These papers are all based on comprehensive personal field work in the southern continents.

The results of the above investigations confirm and elucidate the view of Hooker. Through the reconstruction of the hierarchies involved in the circum-Antarctic distribution patterns formed by the stoneflies and chironomid midges of the southern mountain streams and by the subterranean Bathynellacea of the gravelly beds of those streams, it has been demonstrated conclusively that we are faced with series of monophyletic groups of high age, whose disjunct subgroups are forming orderly, multiple patterns of transantarctic sister-group relationships.

The fact that interstitially living crustaceans of the ground water are involved in transantarctic relationships, stands out as a practically uncontradictable biological proof of the former existence of continuous connections between the southern lands.

Moreover, the structure of the phylogenetic relationships and the patterns of geographical replacement shown by the actual groups give clear evidence of paths and directions of dispersal and of areas of origin, which illustrate important trends in the history of life since the Permian. Fundamental is the insight that there are two main patterns of transantarctic relationship, one of which being formed by groups of southern origin, the other by groups of northern origin.

3.1. — *Circum-Antarctic groups of southern origin.*

Most closely analysed are the subfamilies Podonominae, Aphroteniinae, and Diamesinae among the Chironomidae. They stand out as parts of a world pattern of amphitropical distribution and old transtropic dispersal northwards via East African highlands. The marked primitiveness of the southern representatives is a demonstration of the southern origin of these subfamilies. Against that background it is of interest to note that they still play a prominent quantitative and qualitative role in the fauna of the southern mountain streams.

The following pattern of southern hemisphere relationships is demonstrated by the chironomid midges (Fig. 1-3) : Within each subfamily the group of southern Africa forms the sister group of a

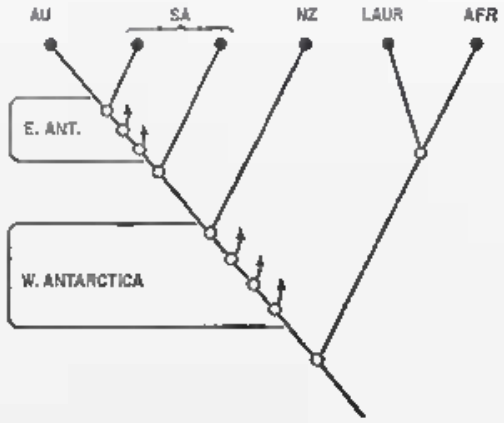

FIG. 1. — The connection between phylogenetic relationship, relative age and geographical distribution in cold-adapted chironomid groups of austral origin. Circles with attached arrows indicate the multiple occurence of accordant transantartic connections within a monophyletic group. The different evolutionary and biogeographical role played by East and West Antarctica after the separation of South Africa from the other southern lands in the Upper Jurassic is also indicated. (From Brundin, 1970.)

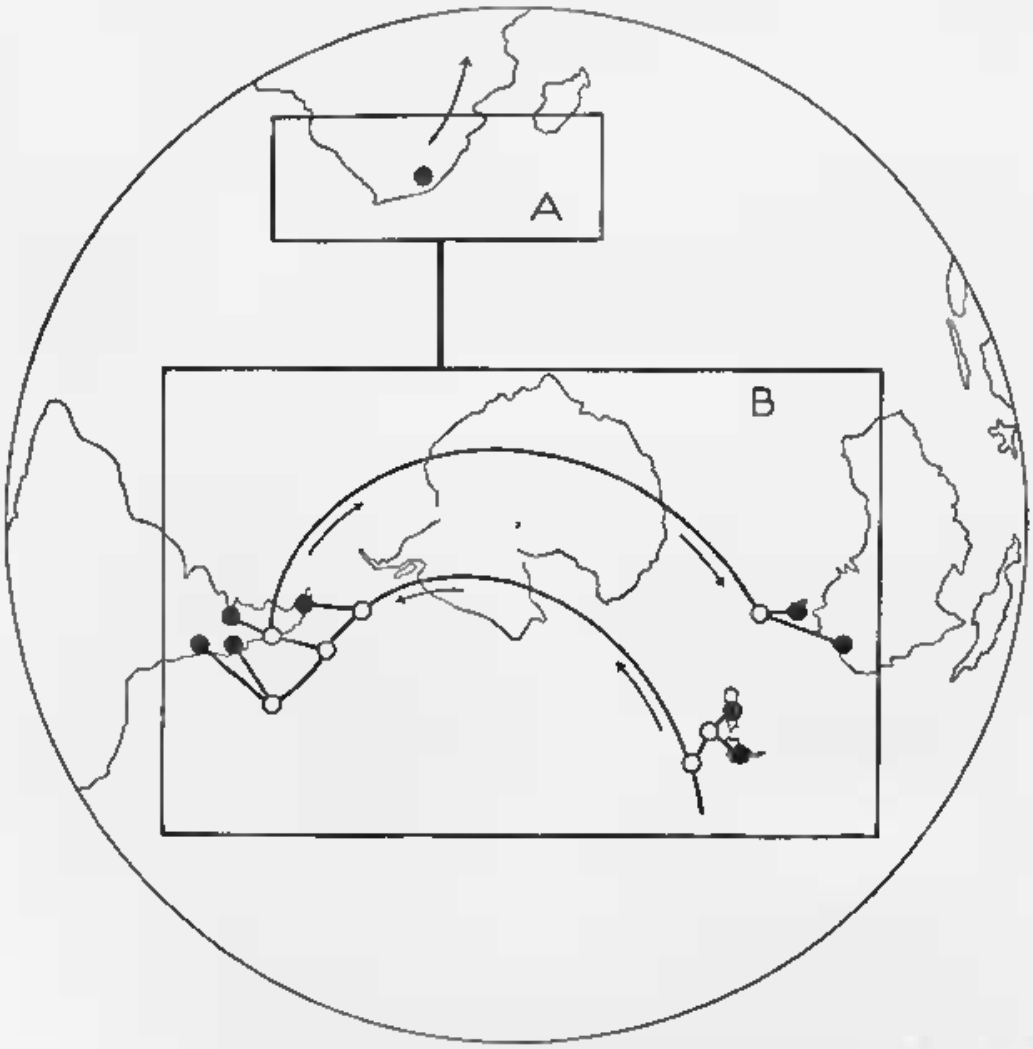

FIG. 2. — Circum-Antarctic distribution and inferred transantarctic dispersal in the subfamily Podonominae (Diptera, Chironomidae). A : the tribe Boreochlini ; B : the tribe Podonomini. The phylogenetic diagram (within the frame of " B ") refers to the situation in the genus *Podonomus*, where the species group of New Zealand is plesiomorphic and the species group of Australia is apomorphic in relation to the corresponding sister groups in South America. (From Brundin, 1972 *a*.)

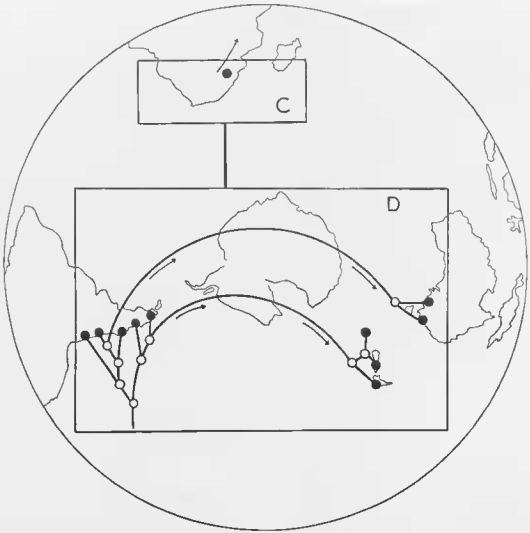

FIG. 3. — Circum-Antarctic distribution and inferred transantarctic dispersal in the subfamily Diamesinae (Diptera, Chironomidae). C : the Diamesae ; D : the Heptagyiae. The phylogenetic diagram (within the frame of " D ") refers to the situation in the tribe Heptagyini, where the group of New Zealand (genus *Maoridiamesa*) and the group of Australia (the *tonnoiri* group of the genus *Paraheptagyia*) are both apomorphic in relation to the corresponding South American sister groups. (From Brundin, 1972 *a*.)

group comprising all the groups of Andean South America, Australia-Tasmania and New Zealand. (Aphroteniinae are not present in New Zealand.) Moreover, within each subfamily all groups of Australia-Tasmania (together 12) and all groups of New Zealand (likewise 12) have their closest relatives, i.e. sister groups, in distant South America.

This pattern is strong indication(1)that direct connections have existed between (southern) Africa and the other southern lands, but that these connections have been cut very early,(2)that there has been a direct connection between Australia, East Antarctica and South America,(3)that another connection between New Zealand, West Antarctica and Andean South America has formed a peripheral arc enabling comparatively independent evolution and dispersal,(4)that the Tasman Sea has functioned as an effective barrier, even to winged chironomid midges.

The junction in southern South America of the two Antarctic routes of dispersal point to the possibility that essential parts of the hierarchies formed by th e recent groups of South America evolved

in Antarctica. Another indication of this may be the fact that the strongly diversified south Andean Podonominae fauna still is quite as richly represented in the Magellanic area (42 species, some endemic) as in the Valdivian area far to the north (43 species).

The multiple transantarctic relationships shown by the stoneflies, all refer to the strictly monophyletic suborder Antarctoperlaria (Zwick, 1969), wich is wholly confined to the southern hemisphere and forms the primitive sister group of the northern suborder Arctoperlaria comprising the rest of the world fauna of Plecoptera. The Antarctoperlarian stoneflies are richly diversified in temperate South America, south-eastern Australia, Tasmania, and New Zealand. But they lack in southern Africa, probably due to extinction caused by climatic changes. Unfortunately, a close comparison with the Chironomidae pattern is not possible, because the relationships of the Antarctoperlarian subgroups of Australia and New Zealand still are not completely known (cf. Zwick, 1969).

However, we learn from the Chironomidae that southern Africa is inhabited by groups of comparatively high age, whose phylogenetic and geographical position is fundamental for an interpretation of the history of the major units. After the isolation of the old African groups of the subfamilies Podonominae, Aphroteniinae and Diamesinae, there must have been comprehensive evolution and dispersal within Antarctica and adjoining continental areas. However, the Australian chironomid groups are all derivative in relation to their corresponding sister groups in South America, which indicates one-way dispersal from East Antarctica to Australia.

This function of Australia as a receiver of derivative southern groups seems to differ strikingly from the picture indicated by the Antarctoperlaria and certain other primitive insect groups, to which Australia evidently has functioned as an important centre of evolution. However, the chironomids are much younger than groups like Plecoptera (see below), and I am tempted to conclude that the role of Australia as an important centre of origin for cold-stenothermal groups had an early maximum during the Permian and Lower Mesozoic and has then declined because of geographical and climatic changes.

Our survey of these matters is still limited. The chironomids are still the only major southern group that has been analysed in detail, and there is reason to expect that equivalent analyses of other groups will reveal the existence of more or less dissimilar patterns. This is first and foremost the case with groups of northern origin which have developed their transantarctic relationships secondarily.

3.2. *Circum-Antarctic groups with northern origin.*

In 1970 I made the supposition that to groups of northern origin, areas to the north of present Australia may have served as a forking point for further dispersal southwards, partly along East Australian highlands, partly along the Inner Melanesian Arc to land areas now represented by New Caledonia and New Zealand. "Dispersal of that kind would give rise to direct sister-group relationships across the Tasman Sea. Given sufficient time and further progression of the groups via West or East Antarctica (or both), the end result of the presupposed transtropic dispersal would be a case of *secondary* transantarctic relationship, in contrast to the *primary* transantartic relationship displayed by groups of southern origin with amphi-Antarctic distribution." (Brundin, 1970.)

Schminke's comprehensive study of subterranean Bathynellacea of the family Parabathynellidae confirms the soundness of the above conception, which does presuppose a pattern of transantarctic relationship just opposite to that one demonstrated by chironomids of southern origin. It is shown by Schminke that the Parabathynellidae had their area of origin in East Asia and that one main branch, reached the Australia-New Zealand sector from the north. There are sister-group relationships and, in one case, species identity across the Tasman Sea. The further dispersal via Antarctica to South America is demonstrated by the *Chilibathynella* group, whose South American species all are derivative in relation to their closest relatives in Australia. Another parabathynellid main branch, the *Ctenobathynella* group, dispersed from Eurasia into tropical Africa and from there into tropical South America. Hence the two parabathynellid branches meet in the latter continent and are represented there by the most derivative species of each.

4. — DISJUNCT GONDWANIC DISTRIBUTION AND CONTINENTAL DRIFT

From the above discussion it is evident that the structure of the phylogenetic relationships existing between the disjunct elements of three different subfamilies among the Chironomidae corresponds well to the quality of the arguments (cf. Hennig, 1960, 1966 *b*) that have to be used as evidence for the former existence of more or less continuous transantarctic migration routes. The picture of Antarctica as an integral part of a former unitary southern centre of evolution is strengthened by the witnesses delivered by the Antarctoperlarian stoneflies. But truly conclusive biological evidence that the southern lands have been connected just according to a Gondwanic pattern is delivered by the Parabathynellidae, not only because these small crustaceans are subterranean, but also because their occurrence in South America is due to separate dispersal partly from Australia via Antarctica, partly from tropical Africa via an area now occupied by the South Atlantic.

However, before we accept the theory that the southern disjunct distribution patterns of Chironomidae, Plecoptera and Parabathynellidae are consequences of the earlier unity and later fractioning of the old Gondwanaland, we are forced to investigate the relation between the absolute age of those groups and the actual geological time scale.

Geologists and geophysists now seem to agree that the disruption of Gondwanaland did not start later than in the Jurassic and that the separation of southern Africa from East Antarctica and the Patagonian block occurred during the Upper Jurassic to Lower Cretaceous (roughly 150-140 million years ago). Disjunct southern groups with occurrence also in southern Africa must be at least of Upper Jurassic age in order to fit confidently into the Gondwanic pattern.

That this requirement is fulfilled by the Chironomidae, has been firmly established through the recent finding of a completely preserved specimen in amber from the lowermost Lower Cretaceous (Neocomian) of Lebanon (Schlee and Dietrich, 1970). The specimen, which is 120-140 million years old, represents an extinct genus of the subfamily Podonominae (cf. above) and seems to be very closely related to the recent *Boreochlus* group of Laurasia. The latter is the derivative sister group of the very primitive *Archaeochlus* group of the Drakensberg (southern Africa). The occurence of a comparatively derivative member of the tribe Boreochlini of the subfamily Podonominae at the northern margin of Gondwana during the Neocomian, proofs that the history of Chironomidae goes well back into the Jurassic (cf. Brundin, 1972 *a*).

However, compared with the Plecoptera and Bathynellacea, the chironomid midges are a fairly young group. We have reason to suppose that the former are both of Upper Paleozoic age. It seems probable that *Stenoperlidium* from the Upper Permian and Upper Triassic of New South Wales represents an extinct subgroup of Antarctoperlaria (Hennig, 1969 : 325). Bathynellacea (Malacostraca : Syncarida) are not known as fossils, but there is strong circumstantial evidence that they are forming one of the oldest groups of the limnic fauna (cf. the comprehensive discussion by Noodt, 1965).

Referring to the above biological evidence, I find that we are forced to conclude that the southern disjunct distribution patterns of chironomid midges, stoneflies, and subterranean crustaceans that have been analysed according to the principles of phylogenetic biogeography, all evolved in direct connection with successive fractioning, by continental displacement, of formerly continuous distribution areas. In other words, the geographical displacements shown by some old groups among the limnic arthropods cannot be explained without reference to the theory of continental drift and plate tectonics. Indeed, there is reason to claim that the special nature of those patterns stands outas strong biological evidence for the soundness of the actual geologic-geophysical theory.

However, before finishing I cannot omit to point at the problem raised by the presence in Australia of members of an " old northern element " (Mackerras, 1970) that is represented by derivative offshoots in South America. If the Bathynellacea are taken as an example of this, I think it must be admitted that their dispersal from East Asia into Australia (resulting in subsequent dispersal via Antarctica to South America) cannot have taken place after the fractioning of Gondwana and the following, post-Eocene contact between Indonesia and Australia-New Guinea. The Bathynellacea case demands continuous connection between South-East Asia and Australia at some point of time

before the start of the fractioning of Gondwana. I am here touching upon a matter where even recent contributions to plate tectonics are of very limited help. In the latest reconstructions of Pangaean geography (cf., for example, Dietz and Holden, 1970, Dewey, 1972), we are faced with a vast gap between South-East Asia and Australia. This seems incompatible with the results of phylogenetic biogeography.

As to these matters, I think the biogeographer cannot but refer to Carey's discussion of plate tectonics and his hypothesis of an expanding globe, that has been supported by Heezen and Holmes (cf. Carey, 1958; Holmes, 1965). Through reversal of the deformations and strains of post-Paleozoic age indicated by orogenic belts, rifts and shear systems, Carey has tried to make a rigorous reconstruction of early Mesozoic paleogeography. With respect to our problem, it is of special interest that Carey's Pangaea shows a close connection between Australia and South-East Asia-Indonesia, which he considers as one of the important results of his analysis (cf. Carey, Fig. 46 c). Carey worked with spherical tracings of the globe, but a general fit of the Pangaean sections was not possible until he assembled his tracings on a globe considerably smaller than the earth of today. On the other hand, when using a globe corresponding to the earth of the present radius, he could reconstruct satisfactorily any sector he might choose but never the whole.

Although there are several problems raised by the theory of plate tectonics that cannot be explained conclusively today, there is evidently good reason to regard it as a major advancement. The young theory is here to stay; and to the biologists the rapidly increasing understanding of how the continents have moved in time and space after the breakup of a single land mass Pangaea, is a challenge calling for intensive, critical exploration of the biogeographical corollaries.

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DISCUSSION

Intervention de M. le Professeur P. G. MARTIN.

I invite Prof. Brundin's comments on the following general propositions.

Suppose two separate continents A and B now contain Sister groups, the group in B being derivative in relation to that in A. There are at least two possible explanations. *First*, the group originated in A and sometime in the past dispersal occurred from A to B. *Second* the groups has a common geographic origin (e.g. in A + B) but since physical separation occurred, continent A has undergone little climatic change while B has changed more.

Further, suppose that A and B were originally in contact, both spread over a range of latitudes from temperate to sub-tropical ; continental drift separated A towards the Equador (so that temperate areas tended to disappear but nat sub-tropical) and B towards A pole (so that sub-tropical areas tended to disappear but not temperate). Then, following drift, temperate groups will tend to remain ancestral in B and derivative in A, while sub-tropical groups will tend to remain ancestral in A and derivative in B.

Le point de vue soutenu par le Professeur L. Brundin en réponse à l'intervention du Professeur P. G. Martin a été inclus dans le texte de sa communication.